

References and Notes

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12. Pieces (5 to 20 g) of sponge tissue collected between 7 and 20 m were incubated aboard ship at constant temperature in 110 ml of filtered seawater in a closed chamber with a magnetic stirrer. Oxygen was measured with a potentiometric oxygen electrode (Yellow Springs Instrument Co., model 53) and a chart recorder. Light from two 600-W tungsten projector lamps was measured with a quantum sensor (Li Cor, Li-185). Photosynthesis and respiration, measured during 20-minute alternating light and dark periods over a period of 2 hours, are expressed as P/R (P , gross production, is the net O_2 produced plus the O_2 respired, and R is O_2 respired). Similar pieces of sponge were incubated simultaneously in filtered seawater with ^{14}C -labeled HCO_3^- ($2 \mu Ci/ml$) for 1 hour, and extracted in a mixture of methanol, chloroform, and water (12:5:3) [R. L. Bielecki and N. A. Turner, *Anal. Biochem.* **17**, 278 (1966)]. After removal by acid of free HCO_3^- , portions of this extract, a 1N KOH digest of the tissue, and the incubation water were tested for radioactivity in PCS II scintillation cocktail (Amersham) using a liquid scintillation counter (Packard Tri-Carb). The potential contribution of cyanobacterial photosynthesis to sponge daily maintenance respiration was calculated by extrapolating instantaneous P/R ratios for daily periods when light exceeded 200 and 400 $\mu E m^{-2} sec^{-1}$, assuming constant respiration.
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Taste Flashes: Reaction Times, Intensity, and Quality

Abstract. Human simple reaction times and magnitude estimates of taste intensity increased as the duration of 500-millimolar sodium chloride or 2-millimolar saccharin sodium pulses lengthened from 100 to 1000 milliseconds. Responses to "What was the taste?" ranged from 94 to 100 percent "sweet" for saccharin and 68 to 83 percent "salty" for salt across all pulse durations when both substances were randomized with water pulses.

We can see much from the light provided during a flash of forked lightning (1), and we can hear an identifiable sound when a twig snaps or when someone gasps. These sensory stimuli, all of which are shorter than 1 second (2), end long before a human gross motor response to them occurs (3). We are thus generally able to detect and identify transient stimuli and unable to respond during or within a few hundred milliseconds of such transients.

What types of responses do humans make to taste stimuli that end before a motor response can be made? We have found that useful taste information is provided by 100-msec gustatory transients, that additional information is obtained during taste stimuli of longer duration, and that lengthy central nervous system processing of gustatory input precedes any behavioral response.

We measured, in volunteer participants (4), reaction times to simple tastes (Fig. 1) and judgments of taste quality (Table 1) and intensity (5) (Table 2) to single pulses of 500 mM NaCl (American

Chemical Society) or 2 mM saccharin sodium (National Formulary) in distilled water (the experimental stimuli), or of distilled water alone (the control stimulus) (6). Pulse durations were 100, 200, 300, and 1000 msec, each presented four times per session in random order, with a 10-second distilled water flow before a pulse and a 5-second flow after (7). Each measurement session began with two practice identified stimulus and control trials. Three or more practice sessions preceded a series of data collection sessions for each type of measurement. Eight control stimuli and eight or more experimental stimuli were given during each session, with at least 60 seconds between stimuli. Both simple reaction times (Fig. 1) and judged stimulus intensity (Table 2) increased with pulse duration. In contrast, no statistically significant change in the taste quality of NaCl or saccharin occurred with change in stimulus duration (Table 1) (8).

Errors on experimental stimulus trials, that is, failure to notice a change in taste, did not exceed 4 percent across all par-

Table 1. Taste quality responses as percentages of total response.

Quality	Stimulus pulse duration (msec)							
	NaCl				Saccharin			
	100	200	300	1000	100	200	300	1000
Salty	68	70	70	83	3	0	0	0
Sweet	0	0	3	0	94	98	100	97
Bitter	13	17	7	7	0	0	0	0
Salty-sour	3	3	10	3	0	0	0	0
Sour	7	0	3	7	0	0	0	0
No change†	3	0	0	0	3	2	0	0
Cinnamon	0	0	0	0	0	0	0	3
Sweet-sour	0	3	0	0	0	0	0	0
Salty-bitter	3	3	7	0	0	0	0	0
Sour-bitter	0	4	0	0	0	0	0	0
Sweet-bitter	3	0	0	0	0	0	0	0

†Experimental stimulus trial error. Such trials were repeated immediately after the next scheduled control stimulus trial in the predetermined random order.

Table 2. Magnitude estimates (median $\pm$ standard error) of the intensity of stimulus pulses of NaCl or saccharin. A 2-second stimulus pulse was assigned a modulus (5) of 20 and used as a standard against which subjects would judge in proportion the intensity of the experimental stimulus. The standard was presented twice before the data collection trials began and then after every five trials during the session. Participants served in each of five separate data collection sessions for NaCl and for saccharin. Intensities of all possible pairings of NaCl pulses were significantly different (Wilcoxon matched-pairs signed-ranks test), except for pairs 100–300 and 200–300 msec, at both measurement times. For saccharin, all pairs were different except 100–300, 100–200, and 200–300 msec.

Time	Stimulus pulse duration (msec)							
	NaCl				Sodium saccharin			
	100	200	300	1000	100	200	300	1000
Last 100 msec of pulse	11 $\pm$ 0.1	14 $\pm$ 0.7	12 $\pm$ 0.9	18 $\pm$ 1.0	8 $\pm$ 1.8	12.5 $\pm$ 1.5	10.5 $\pm$ 1.2	1.6 $\pm$ 1.4
5 seconds after pulse	3 $\pm$ 1.2	5 $\pm$ 0.9	4.5 $\pm$ 0.9	7 $\pm$ 1.4	3 $\pm$ 0.9	3 $\pm$ 1.2	3 $\pm$ 0.9	6 $\pm$ 1.2

participants for any NaCl pulse duration or type of response, whereas errors were below 10 percent for the three longer saccharin stimulus durations. For the 100-msec saccharin pulses, failures to report a change in the taste quality were rare (3 percent) in quality judgment sessions, but failures to report a change in taste intensity (14 percent) and to respond on reaction time trials (20 percent) were more frequent. Since relatively high experimental stimulus concentrations were selected to facilitate detectability, the error rates for the 100-msec saccharin pulses suggest decreased sensory information at this brief duration. On control stimulus (water) trials, no error rates exceeded 10 percent for any type of measurement session or pulse duration (9).

In agreement with previous studies, the simple taste reaction times were all more than 400 msec long (4, 10, 11) and were longer for saccharin than for NaCl (10). No liquid taste stimuli with durations below reaction times have previously been used with human judgments of the intensity and quality of the stimuli. Consequently, the tripartite observation that 100-msec pulses (i) permit reaction times of "normal" speed and variability, (ii) lead to quality categorizations comparable to those for long pulses, and (iii) elicit consistent judgments of intensity, is important. It indicates that the sensory response to this brief gustatory pulse, which in the primary nerves reaching the tongue's taste receptors may be only a phasic transient (12), contains considerable information. In addition, it confirms previous suggestions that only a small part of human taste reaction time (11) is attributable to a necessary input (4) or action time (13). Latency of gustatory neural responses is in general somewhat longer than that for visual or auditory responses in vertebrates, but only by 10 to 25 msec (12). Human gustatory neural response latencies are not known, but rise times of human peripheral gustatory neural responses are comparable to

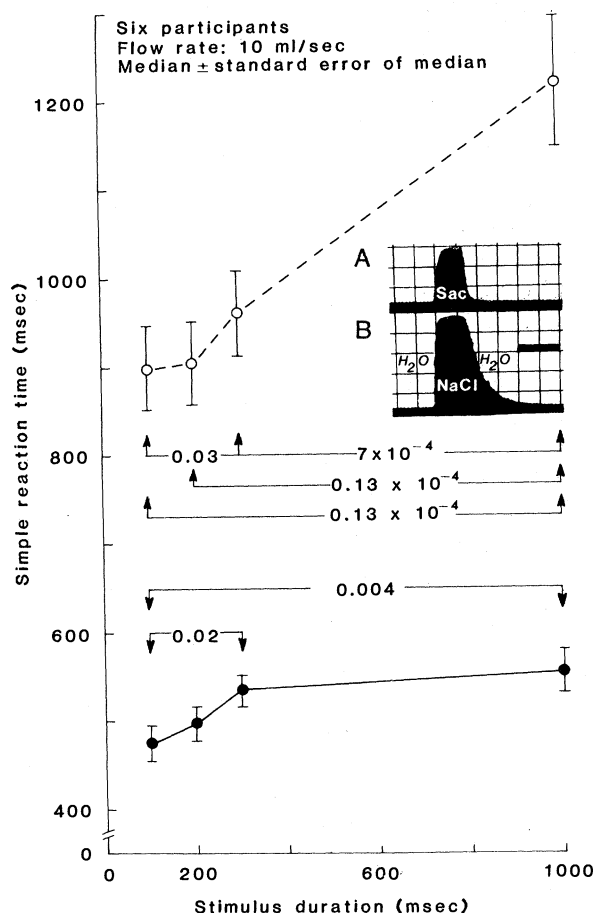
those of other mammals (14). Consequently, it may be that much of the 200-msec (or longer) difference between simple auditory or visual reaction time and simple taste reaction time is due to longer central nervous system processing of the sensory input. The apparent longer processing may indicate the complexity of the judgment. However, some part of the time difference may be a delay normally related to movement of the tongue.

Previous investigations using gustatory stimulus durations of 700 msec or longer found that judged taste intensity increased with duration (15). Our data show this trend for stimulus durations several hundred milliseconds below the gustatory reaction time range. Similarly,

a direct relationship between stimulus duration and judged intensity occurs in vision (16). In general, this observation demonstrates that, over some range, an increase in the duration of sensory stimulation increases the information available to and used by the organism. For taste in particular, one implication is that not all information for intensity is provided by the phasic portion of the sensory neural response. Judged intensity almost doubled when the gustatory pulse was lengthened from 100 to 1000 msec (Table 2). Thus, brief taste pulses do not evoke responses comparable to those which would be produced in normal liquid ingestion (17).

The increase in reaction time with

Fig. 1. Median ($\pm$ standard error) time from onset of a taste stimulus (open circles, saccharin; filled circles, NaCl) to the report of any taste change. The connected arrows (downward for NaCl, upward for saccharin) identify statistically significant ($P < .05$, two-tailed Wilcoxon matched-pairs signed-ranks test) differences between reaction times to each duration. The insert shows solution conductivity, measured on calibration trials with a flow-through conductivity cell (4, 17) located 2.5 mm past the end of the opening to the tongue chamber, before, during, and after 100-msec experimental stimulus pulses of saccharin (A) or NaCl (B). Calibration in the inset, 100 msec.



longer stimulus durations was unexpected but not unprecedented. The explanation offered for this type of increase with duration of visual and auditory stimuli assumes that the longer durations "... lengthen reaction time rather than make it faster by providing the subject with an opportunity to take a longer sample of sensory information than is necessary..." (18). This explanation seems appropriate for our taste data (Fig. 1) and is supported by the increase in judged intensity with longer pulses (Table 2). Since the latency of the peripheral neural response cannot be posited as a possible reason for the increases in reaction time, the concept of greater information at the longer durations fits both the intensity judgment and the reaction time observations. However, since a high sensitivity to changes over time in the concentration of gustatory stimuli has been observed (17, 19), with maximum sensitivity at ≤ 1 Hz (19), the long reaction times to our 1000-msec pulses may be related to the separation between ON and OFF with such pulses.

The data demonstrate a substantial human capacity not only to respond to, but also to receive qualitative and quantitative information from relatively brief taste pulses. The generality of these data is limited by our use of only single, relatively high, concentrations of two substances (10, 11). Nonetheless, it seems that the long human taste reaction times are not caused by a requirement for stimulus durations almost as long, and the initial phasic portion of the human peripheral gustatory neural response is likely to contain appreciable, but far from complete, information on the stimulus.

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2. The sounds of a dry twig snapping or a human gasping last 100 to 150 msec.
3. Minimum human simple visual or auditory reaction times requiring a finger movement are 140 to 220 msec [A. T. Welford, Ed., *Reaction Time* (Academic Press, London, 1980), pp. 1-330].
4. Participants were six paid volunteers (ages 20 to 27) who passed a screening task used in a taste reaction time experiment for reliability of taste judgments [B. Lester and B. P. Halpern, *Physiol. Behav.* **22**, 391 (1979)].
5. Two magnitude estimates [S. S. Stevens, *Psychol. Rev.* **78**, 426 (1971)] were obtained during each intensity session trial, one 100 msec before the end of the pulse and the other 5 seconds after the end of the stimulus pulse. These estimates were signaled for by one or two 100-msec, 2600-Hz sounds produced by solid-state transducers

- operated by a programmable controller, which ran each trial.
6. Conductivity, $< 1.8 \mu\text{S}$; refractive index, 1.3330.
 7. Liquids reached the tongue through a 10-mm by 5-mm elliptical opening in the bottom wall of a polypropylene tube and continued in the tube past the tongue. The anterior dorsum of the tongue was pressed up against a silicon rubber bead around the opening, with the anterior tip of the tongue contacting a tongue reference point located at the rear margin of the rubber bead. Participants pressed their upper central incisors down on a Plexiglas rod. On the outside of the liquid delivery tube, a distilled water flow at 9.4 ml/sec provided a surround rinse around the tongue opening. A median concentration of 4-mM NaCl (below human taste threshold [M. O'Mahony, *Perception* **8**, 441 (1979)]) was measured in the surround rinse liquid during the flow of 500-mM NaCl through the delivery tube and over the tongue.
 8. Kramer test, $P > .05$ [A. Kramer, G. Kahan, D. Cooper, A. Papavasiliou, *Chem. Senses Flavor* **1**, 121 (1974)]. χ^2 (24) = 19.63, $P > .75$. When all quality category columns other than salty and bitter were combined so that all expected frequencies were > 1 and only 25 percent of the cells had expected frequencies < 5 , χ^2 (6) = 5.385, $P > .75$.
 9. An error on a control trial occurred when a change in taste was reported for the control (water) pulse. Control error rates for 100-, 200-, 300-, and 1000-msec pulses were 0, 2, 2, and 2 percent for NaCl, 0, 0, 6, and 0 percent for saccharin across magnitude estimate sessions; 4, 0, 6, and 2 percent across quality category sessions; 8, 10, 7, and 5 percent across all reaction time sessions.
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 12. Typical mammalian chorda tympani nerve response latencies to chemical stimulation of the

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 16. For durations below some critical value, Visual intensity reaches a maximum, and then decreases, as flash duration exceeds 80 to 150 msec [L. A. Riggs, in *Woodworth and Schlosberg's Experimental Psychology*, J. W. Kling and L. A. Riggs, Eds. (Holt, Rinehart, Winston, ed. 3, New York, 1971), pp. 273-314].
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A Benzodiazepine Receptor Antagonist Decreases Sleep and Reverses the Hypnotic Actions of Flurazepam

Abstract. The benzodiazepine receptor antagonist 3-hydroxymethyl- β -carboline, which blocks several of the pharmacological actions of benzodiazepines, induces a dose-dependent increase in sleep latency in the rat. Furthermore, at a low dose that by itself does not affect sleep, 3-hydroxymethyl- β -carboline blocks sleep induction by a large dose of flurazepam. The benzodiazepine receptor may play a role in both the physiological regulation and pharmacological induction of sleep.

Benzodiazepines are widely used in the treatment of insomnia, anxiety, seizures, and muscle disorders. In recent years a single benzodiazepine, flurazepam, has accounted for about half of all hypnotic prescriptions in the United

States (1). The excellent correlations between the affinity of a series of benzodiazepines for specific receptor sites in the mammalian central nervous system and the potency of these compounds as anxiolytics, anticonvulsants, and muscle re-

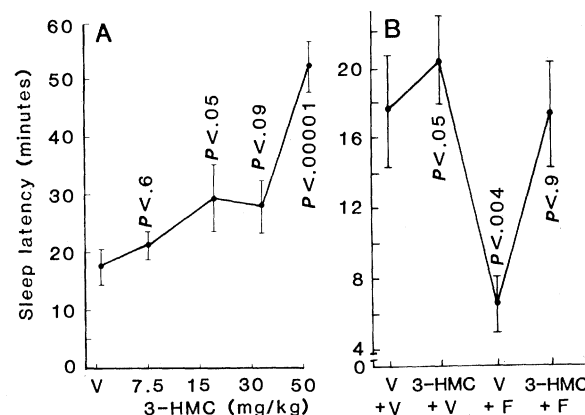


Fig. 1. (A) Effects of 3-HMC on sleep latency. The rats were administered 3-HMC at 0900 hours, and 5 minutes later EEG recordings were made for 2 hours. Overall significance by ANOVA was $P < .00001$. (B) Effects of 3-HMC on the hypnotic actions of flurazepam. The rats were administered vehicle or 3-HMC (7.5 mg/kg) 5 minutes before receiving vehicle or flurazepam (40 mg/kg). EEG recordings were performed for 2 hours after the last injection, beginning at 0905. Overall significance by ANOVA: $P < .003$. Abbreviations: V, vehicle; F, flurazepam.